WHITE ASH (*FRAXINUS AMERICANA* L.) SURVIVAL AND GROWTH IN UNMANAGED UPLAND FORESTS

Jeffrey S. Ward[1]

Abstract: Crown class and diameter of 704 white ash (*Fraxinus americana* L.) > 0.5 inches dbh have been monitored at 10-yr intervals since 1927. Nominal stand age was 25 years in 1927. Although the density of white ash in the upper canopy declined from 14/acre to 3/acre between stand ages 25 through 85, the proportion of the upper canopy comprised by white ash only fell from 5.2% to 3.6%, respectively. In contrast, both absolute and relative density of lower canopy fell precipitously between stand ages 25 to 85, from 53/acre (4.5%) to 3/acre (0.5%). White ash ingrowth has never exceeded 2.6 trees/acre/decade. Survival and growth of white ash in 25- to 85-yr-old stands were influenced by crown class and disturbance. Mortality was negatively correlated with crown class. Mortality of suppressed trees was 3-5x higher than for trees in the upper canopy. Mortality and diameter growth were independent of tree diameter when crown class effects were removed. Over the 60-yr period, diameter growth for upper canopy, intermediate, and suppressed crown classes averaged 0.8", 0.4", and 0.2"/decade, respectively. Because of low recruitment and lower canopy survival, white ash will likely decline in these forests without periodic disturbances.

INTRODUCTION

White ash (*Fraxinus americana* L.) is one of the most widespread species in the United States and be found in every state east of the 95th meridian (Schlesinger 1990). There has been concern about a white ash 'decline' and increased mortality since at least the early 1960s (Han and others 1991, Smallidge and others 1991a,b). However, there is very little information on mortality and growth rates of white ash during stand development.

Earlier studies have reported that mortality rates for white ash differ among crown classes. The 10-yr mortality rates ranged from 0.7-3.1% for upper canopy trees, and 23-100% for suppressed trees (Table 1). However, these studies, and studies with mixed crown classes, do not provide information on whether mortality changes during stand development. The rate at which white ash ascends into the upper canopy, or regresses into lower canopy positions is even less well documented.

Fewer studies have documented diameter growth rates (Table 1). Many have small sample sizes. Only one study documented the diameter growth of suppressed white ash (Burns and White 1930). Fastest diameter growth appears to occur between stand ages 25-60, 1.2-3.0 inches/decade. Diameter growth is approximately 1.2 inches/decade in second-growth stands and 1.5 inches/decade in 'old-growth' stands. Unfortunately, these studies do not report basal area growth rates that may be a more appropriate indicator of individual tree vigor.

The objective of this paper is to document development of white ash during natural succession in unmanaged southern New England forests. Individual trees have been inventoried at 10-yr intervals over a 60-yr period in four unmanaged stands in Connecticut. The study includes 704 white ash trees. The long-term monitoring of individual trees permitted an examination of the influence of individual tree characteristics on white ash development. Specifically, this study examined the influence of crown class and diameter class on survival, movement among crown classes, and diameter growth of white ash between stand ages 25-85 yr.

[1]Department of Forestry and Horticulture, The Connecticut Agricultural Experiment Station, 123 Huntington Street, New Haven, CT 06504-1106, Phone: (203) 789-7238, FAX: -7232.

Table 1. Summary of previous research on white ash 10-yr mortality rate (%) and diameter growth (inches/decade) by initial stand age and crown class

Source	Notes[1]	Initial age[2]	Crown/dbh class[3]	Sample size	Study length	10-yr rate	
						Mortality[4]	Dbh[5]
Lorimer 1984	i	37	Sup	109	4	34.2	-
Lorimer 1984	i	42	Sup	92	14	76.38	-
Lorimer 1984	i	67	Sup	11	13	100.0	-
Burns and White 1930	t	SG	Sup	12	11	23.0	0.3
Conover and Ralston 1959	t	11	Upp	248	16	2.8-6.3	2.0-3.1
Lorimer 1984	i	37	Upp/Int	103	4	0.0	-
Lorimer 1984	i	42	Upp/Int	103	14	41.8	-
Zarnovican and Laberge 1994	i	52	Upp	26	4	-	1.2
Burns and White 1930	t	SG	Upp	71	11	11.6	0.7
Hibbs 1983	p	10	n/a	1360	30	45.3	-
Elliott and Swank 1994	p	12	≥ 2"	28	7	29.1	-
Marquis 1969	e,t	25	3-5"	n/a	5	-	1.5-2.6
Schlesinger 1990	n/a	28-38	n/a	n/a	n/a	-	1.2-2.0
Schlesinger 1990	n/a	20-60	n/a	n/a	n/a	-	2.0-3.0
Leak 1970	i	40-60	n/a	n/a	8-13	5.5-7.8	-
Leak 1970	i	40-70	n/a	n/a	8-13	4.4-17.5	-
Wilson 1953	t	65	5-16"	~40	10	-	1.2
Christensen 1977	p	120	n/a	7	22	14.2	-
Pallardy and others 1988	p	SG	< 3.5"	93	14	21.4	-
Volk and Fahey 1994	i	SG	n/a	194	53	7.6	-
Fain and others 1994	p	SG	n/a	>700	53	2.3	-
Teck and Hilt 1990	i	n/a	5-27"	2028	4-17	10.2	-
Schlesinger 1990	n/a	SG	n/a	n/a	n/a	-	1.2-3.1
Runkle and Yetter 1987	i	SG	n/a	3	7	-	1.3
Teck and Hilt 1991	i	n/a	5-27"	1782	4-17	-	1.4
Newman and Ebinger 1985	p	OG	1-4"	46	18	64.9	-
Parker and others 1985	i	OG	4-8"	24	50	7.8	1.68
Parker and others 1985	i	OG	8-12"	45	50	29.2	1.83
Parker and others 1985	i	OG	12-16"	91	50	22.8	1.17
Parker and others 1985	i	OG	16-20"	73	50	13.7	1.48
Parker and others 1985	i	OG	≥ 20"	25	50	16.7	1.37
McGee 1984	e	OG	> 9"	275	8	6.1-7.2	-
Leak 1970	i	OG	n/a	n/a	8-13	1.8-3.3	-

[1] e=estimate, i=individual tree, p-=ate of population decrease, t=thinning study, n/a=not available.
[2] SG=second growth, OG=old growth.
[3] Upp=Upper canopy, Int=intermediate, Sup=suppressed.
[4] Converted to 10-yr rates (%) using $(1-(1-m)^{(10/y)})$ where m=published mortality rates and y=length of study in years.
[5] Diameter growth (inches/decade).

Study Areas

Study areas are located in the Cabin (40 acres), Cox (50 acres), and Reeves Tracts (40 acres) in Meshomasic State Forest, and the Turkey Hill Tract (80 acres) in Cockaponset State Forest. Most of the land where the plots are located was cleared for farming during the early 1800s and abandoned by the late 1800s. The present forests developed following clearcutting of the second forest for charcoal production around 1900. Prior to fire suppression programs begun during the 1920s, the forests were repeatedly burned to improve grazing and clear brush.

Soils are very stony to extremely stony, fine sandy loams derived from gneiss and schist glacial till with scattered rock outcrops. Topography is gently rolling. Elevations range from 280-650 feet m.s.l. Climatic data are from Hartford, Connecticut, approximately 16 miles northwest of the Meshomasic plots. The area is in the northern temperate climate zone with average annual precipitation of 44 inches (National Oceanic and Atmospheric Administration 1991).

Stand composition and structures are typical of second-growth southern New England forests: upland oak (*Quercus* spp.) in the upper canopy and a lower canopy comprised mostly of maple (*Acer* spp.) and birch (*Betula* spp.). Upland oaks have accounted for more than half the upper canopy basal area since the first inventory (Stephens and Ward 1992). The mean diameter of upper canopy trees increased from 5.1 inches in 1927 to 13.6 inches in 1987 (Ward and Stephens 1994). Study areas were repeatedly defoliated by gypsy moths (*Lymantria dispar*) between 1961-1964, 1971, and 1981. These defoliations greatly increased mortality of upland oak, but not maple and birch (Stephens 1981).

METHODS

Field Measurements

The Turkey Hill Tract was established in 1926, and the Cabin, Cox, and Reeves Tracts in 1927. Median age of upper canopy northern red oak (*Quercus rubra*) was 80 years in 1983. The approximate stand age at each measurement, rounded to nearest 5th year, is used rather than the measurement year to facilitate relating results to stages in stand development. Stand ages 25, 35, 55, 65, 75, and 85 will refer to measurements in 1927, 1937, 1957, 1967, 1977, and 1987 respectively.

Trees were mapped to the nearest link (7.92 inches) on transect segments one chain (66 feet) long by 16.5 feet wide. Each transect segment was 1/40 acre. Each tract had 6 to 14 transects and each transect had 10 to 20 transect segments. Transects were spaced at four chain intervals on Cabin, Cox, and Reeves Tracts and five chains intervals on the Turkey Hill Tract. The centerline of each transect was permanently located by a stake and rock cairn at two chain intervals. This study used the 364 transect segments (9.1 acre) that have not been disturbed since 1927. Segments that have been disturbed by partial cutting, road and trail construction, or fire were excluded (3.7 acre).

Transect maps were used to relocate trees in the subsequent inventories of 1937 and 1957. Trees have been relocated since 1967 using the distance along the centerline together with the tree's position right or left of centerline. During each inventory, the species, diameter, and crown class of each tree was recorded. Minimum dbh (diameter at 4.5 feet) was 0.6 inches before 1957; since 1957 the minimum dbh has been 0.5 inches. A metal tape was stretched between stakes to relocate the centerline of each transect segment. Individual trees were matched with data from previous inventories using their location, species, and diameter. New (ingrowth) trees were recorded during each inventory. Inconsistent data (including large ingrowth) were field checked after each inventory to ensure data quality. Crown class designation standards in 1927 and 1937 were based on Fernow (1917), which are nearly identical to those used in later surveys (Smith 1962).

Data Analysis

Data from the four tracts, which had similar histories, soils, compositions, and climate, were pooled to simplify the analysis. Antecedent crown class is defined as the crown class at the beginning of a period. Four crown class transitions were recognized: ascension (moved into a higher crown class during period), persistence (remained in same crown class), regression (moved into a lower crown class), and mortality.

Crown class transition rates were defined as the proportion of trees in a given antecedent crown class that exhibited crown class ascension, regression, persistence, or mortality during a period. Ten-yr crown class transition matrices were created and squared to obtained 20-yr crown class transition rates for the periods between stand ages 25-35, 55-65, 65-75, and 75-85. This permitted a direct comparison of rates for the 1937-1957 period (stand ages 35-55) with rates for the other periods. Mortality rates were converted to 10-yr mortality rates, as described above, to allow a direct comparison with published rates. Differences in crown class transition rates among periods for each antecedent crown class were tested using procedures in Neter and others (1982, p. 325-329). Differences were considered significant at $P < 0.05$.

A one-way ANOVA with diameter as the dependent and crown class as the categorical variable was used to determine the correlation between crown class and diameter at stand ages 25 and 55 years. To assess the influence of crown class independently of diameter, trees measured at stand age 25 and 55 years were assigned to 3 diameter classes: 0.5-1.9, 2.0-5.9, and >6.0 inches dbh. The Mantel-Haenszel test (SYSTAT 1992) was used to determine whether mortality between stand ages 25-55 and 55-85 was independent of canopy class (upper vs. lower canopy) when stratified by diameter class, and diameter class when stratified by crown class. Differences were considered significant at $P < 0.05$.

Analysis of variance was used to examine influence of crown class and stand age (fixed effects) on diameter growth with initial diameter as a covariates on diameter growth. Tukey's HSD test was used to determine whether diameter growth differed among crown and diameter classes within and among intersurvey intervals. Differences were considered significant at $P < 0.05$.

RESULTS

White ash density steadily declined over the past 60 years, from 67 stems/acre at stand age 25 to 6 stems/acre at stand age 85 (Table 2). Concurrently, dispersal of white ash decreased from 40% of transect segments at stand age 25 to 11% at stand age 85. Most of the decline has occurred in the suppressed and intermediate crown classes. Lower canopy density decreased 94% between stand ages 25 to 85. Although the density of upper canopy white ash decreased 76% between stand ages 25-85, the proportion of the upper canopy comprised of white ash only decreased from 5.2% to 2.6%. White ash ingrowth has averaged less than 2.5 trees/acre/decade.

Crown Class Transitions

Survival and crown class transitions of white ash were not independent of antecedent crown class. The distribution of trees among crown classes at the end of a period (including mortality) was not independent of antecedent crown class for each of the five periods (stand ages 25-35, 35-55, 55-65, 65-75, and 75-85). Chi-square values (χ^2) for all periods were highly significant ($p < 0.001$).

Table 2. Stand density (stems/acre), mean dbh (inches), ingrowth (stems/acre/decade), and frequency of white ash in Connecticut by crown class and stand age

Crown class	Stand age (yr)					
	25	35	55	65	75	85
			Density (stems/acre)			
Upper canopy	11.3	6.5	4.3	5.2	3.8	2.7
Intermediate	14.8	7.9	2.7	2.4	1.1	1.0
Suppressed	40.5	28.8	12.1	3.8	2.6	2.0
Combined	66.7	43.2	19.1	11.4	7.6	5.7
			Mean diameter (inches)			
Upper canopy	4.5	6.3	8.0	8.2	9.5	11.0
Intermediate	2.4	3.9	5.3	5.2	6.1	7.0
Suppressed	1.2	1.9	2.0	1.3	1.4	1.5
Ingrowth	-	2.3	2.6	0.9	1.3	0.9
Frequency [1]	39.8	34.1	22.3	16.2	12.6	11.0

[1] Percent of transect segments (1/40 acre) with at least one white ash.

Crown class ascension rates were not stationary from stand ages 25 through 85 (Table 3). The crown class ascension rate of intermediate trees between stand ages 55-65 was 3-21 times higher than earlier or later periods. This rate was significantly higher than for all other periods except stand ages 75-85. The crown class ascension rate of suppressed trees also peaked between stand ages 55-65. This rate was 4-9 times higher for other periods and significantly higher than for earlier periods. Intermediate trees moved into the upper canopy at higher rates than suppressed trees moved into the intermediate crown class during all periods (Table 3).

Two general pattern of crown class persistence were noted (Table 3). Persistence of white ash in upper canopy and the intermediate crown class peaked between stand ages 55-65. Nearly 96% of white ash in the upper canopy at stand age 55 remained in the upper canopy through stand age 65. The opposite pattern was observed for trees in the suppressed crown class. Crown class persistence between stand ages 55-65 was significantly lower than for the previous 30 years because crown class ascension greatly increased. Persistence of intermediate trees was lower than for upper canopy trees for all periods, and lower than for suppressed trees for all periods except between stand ages 55-65.

Temporal patterns of crown class regression were similar for upper canopy and intermediate white ash (Table 3). Crown class regression rates were higher between stand ages 25-55 than for the next 30 years. Regression rates were at their lowest between stand ages 55-65, the period of defoliation and drought. Regression rates began to rise after stand age 65, but still were much lower than prior to stand age 55. Crown class regression rates of intermediate trees was lower than for upper canopy trees for all five periods.

Table 3. 20-yr crown class transition rates (%) for white ash in Connecticut by antecedent crown classes among stand age intervals. Column values with same letter for a given crown class were not significantly different at $p < 0.05$.

Crown class at beginning of period	Period (stand age)	20-yr crown class transition rate (%)					
		Ascension		Persistence		Regression	
Upper canopy	25-35	-		28.6	a	56.7	c
Upper canopy	35-55	-		52.5	b	28.8	b
Upper canopy	55-65	-		95.9	c	3.3	a
Upper canopy	65-75	-		49.9	b	10.5	ab
Upper canopy	75-85	-		47.2	ab	19.1	b
Intermediate	25-35	2.2	a	6.3	a	36.5	b
Intermediate	35-55	6.9	ab	11.1	a	22.2	b
Intermediate	55-65	46.6	c	11.2	a	0.0	a
Intermediate	65-75	3.6	ab	1.9	a	6.9	ab
Intermediate	75-85	15.1	bc	5.8	a	8.7	b
Suppressed	25-35	1.1	a	18.59	b	-	
Suppressed	35-55	1.1	a	17.56	b	-	
Suppressed	55-65	10.2	b	6.48	a	-	
Suppressed	65-75	1.2	ab	8.68	ab	-	
Suppressed	75-85	2.6	ab	11.94	ab	-	

Mortality

The mortality rate of upper canopy white ash has always been significantly lower for intermediate and suppressed trees (Table 4). The rate for intermediate trees was significantly higher than for suppressed trees prior to stand age 65. Two general temporal patterns were noted for mortality when trees were segregated by crown class. Mortality rates of suppressed white ash increased slightly, but not significantly, between stand ages 25-85 (Table 4). There was also a long term trend of increasing mortality rates for both intermediate and upper canopy trees. Mortality rates for both crown classes were significantly higher between stand ages 75-85. In contrast with the pattern for suppressed white ash, mortality rates for the higher crown classes decreased between stand ages 55-65 (Table 4).

Mortality decreased with increasing tree diameter (Table 4). Crown class and diameter were highly correlated at stand age 25 ($r^2 = 0.498$, $p<0.001$). White ash mortality between stand ages 25-55 was independent of diameter class when crown class effects were removed (Mantel-Haenszel $\chi^2 = 3.04$, $p<0.081$), but not independent of canopy class (upper vs. lower canopy) when diameter class effects were removed (Mantel-Haenszel $\chi^2 = 44.95$, $p<0.001$). Therefore, mortality estimates based on diameter were improved by also using canopy class, but mortality estimates based crown class alone were not improved by also using diameter. Similar relationships were noted between stand ages 55-85. Crown class and diameter were highly correlated at stand age 55 ($r^2 = 0.617$, $p<0.001$). Mortality of white ash between stand ages 55-85 was independent of diameter class when crown class effects were removed (Mantel-Haenszel $\chi^2 = 0.22$, $p<0.638$), but not independent of canopy class when diameter class effects were removed (Mantel-Haenszel $\chi^2 = 25.12$, $p<0.008$).

Table 4. Significance of 10-yr mortality rates (%) for white ash in Connecticut among periods (stand age intervals) by crown and diameter classes.

	Period (stand age)									
	25-35		35-55		55-65		65-75		75-85	
	Significance among periods[1]									
Upper canopy	7.7	b	9.8	bc	0.4	a	21.1	d	18.6	cd
Intermediate	32.9	a	36.5	a	24.0	a	64.8	b	45.6	ab
Suppressed	55.7	a	56.8	a	59.2	a	68.6	a	61.8	a
> 6.0" dbh	4.2	a	14.4	ab	4.8	a	26.1	b	18.4	b
2.0-5.9" dbh	24.2	a	45.0	b	52.6	b	58.0	b	50.0	b
0.5-1.9" dbh	58.2	a	56.8	a	64.3	a	63.0	a	58.1	a
	Significance among classes[2]									
Upper canopy	a		a		a		a		a	
Intermediate	b		b		b		b		b	
Suppressed	c		c		c		b		b	
> 6.0" dbh	a		a		a		a		a	
2.0-5.9" dbh	b		b		b		b		b	
0.5-1.9" dbh	c		c		b		b		b	

[1] row values with the same letter were not significantly different at $p \leq 0.05$.

[2] column values with the same letter were not significantly different at $p \leq 0.05$ than between stand ages 25-35.

Diameter Growth

Diameter growth (inches/decade) was significantly different among crown classes ($F=65.3$, d.f.=2, $p<0.001$), and diameter classes ($F=29.1$, d.f.=2, $p<0.001$). Mean diameter growth was significantly greater for trees in the upper canopy than for suppressed trees, 0.78 and 0.25 inches/decade, respectively. Mean diameter growth was significantly greater for larger white ash (> 6" dbh) than for smaller trees (0.5-1.9" dbh), 0.75 and 0.31 inches/decade, respectively. After stand age 65 diameter growth was independent of diameter, but not crown class. Within a crown or diameter class, diameter growth was constant between stand ages 25-85 (Table 5).

DISCUSSION

The crown class of an individual white ash had a strong influence on future survival and development of that tree. For example, while 25.2% of upper canopy trees in the 25-yr-old stand survived through stand age 85, and 17.5% remained in upper canopy positions, only 2.2% of intermediate trees survived between stand ages 25 to 85. Therefore, number of white ash that can be expected in future stands depends on both the number of trees and their distribution among the crown classes. Thirty-year crown class transition values (stand ages 25-55) were calculated from the data to facilitate comparison with earlier reports on other species. The results show that 332 upper canopy or 6,757 intermediate white ash at stand age 25 are necessary to obtain 100 upper canopy trees at stand age 55. This compares with 550 and 1,730 for yellow birch (*Betula alleghaniensis*), 440 and 3,570 for red maple (*Acer rubrum*), and 170 and 1,200 for northern red oak (Ward and Stephens 1993, 1994). White ash is more likely to remain in the upper canopy on these sites than red maple or yellow birch, but not northern red oak. However, white ash is much less likely to ascend from the intermediate crown class into upper canopy positions than the other co-occurring species.

Table 5. Significance of diameter growth rates (inches/decade) for white ash in Connecticut among periods (stand age intervals) by crown and diameter classes

	Period (stand age)									
	25-35		35-55		55-65		65-75		75-85	
	Significance among periods[1]									
Upper canopy	0.88	a	0.62	a	0.77	a	0.71	a	0.88	a
Intermediate	0.44	a	0.32	a	0.49	a	0.23	a	0.32	a
Suppressed	0.27	a	0.22	a	0.21	a	0.25	a	0.22	a
> 6.0" dbh	1.01	a	0.74	a	0.63	a	0.73	a	0.85	a
2.0-5.9" dbh	0.68	a	0.36	b	0.51	ab	0.39	ab	0.33	ab
0.5-1.9" dbh	0.32	a	0.29	a	0.20	a	0.28	a	0.30	a
	Significance among classes[2]									
Upper canopy	a		a		a		a		a	
Intermediate	b		b		ab		a		ab	
Suppressed	b		b		b		a		b	
> 6.0" dbh	a		a		a		a		a	
2.0-5.9" dbh	a		b		ab		a		a	
0.5-1.9" dbh	b		b		b		a		a	

[1] row values with the same letter were not significantly different at $p \leq 0.05$.
[2] column values with the same letter were not significantly different at $p \leq 0.05$.

A significant advantage for white ash that ascend to upper canopy positions is reduced mortality rates relative to trees in subordinate canopy positions (Table 4). This has been true for the entire 60 years of this study and is consistent with earlier reports (Lorimer 1981, 1984). The mortality rates observed in this study are comparable with those in earlier reports (Table 1). Upper canopy mortality rates of this study (1-21%/decade) were somewhat higher than published rates (3-12%/decade). Mortality rates of suppressed trees were more consistent than earlier studies (56-69%/decade vs. 23-100%/decade, respectively).

White ash is highly resistant to gypsy moth defoliations (Herrick and Gansner 1987, Liebhold and others 1995). During the period of repeated defoliations, between stand ages 55-65, mortality rates fell sharply for intermediate and upper canopy white ash (Table 4). This is in marked contrast to the sharply increased mortality of upper canopy northern red oak during the same period (Ward and Stephens 1994). The sharp increase in crown class ascension rates during the decade of defoliation (Table 3) indicates that lower canopy white ash respond rapidly to release. Crown class regression rates increased following subsidence of defoliation intensity, but at lower rates than before stand age 55. Considering the decreased mortality and crown class ascension rates, it is surprising that there was not a concurrent increase in diameter growth (Table 5).

The very low density of white ash ingrowth (Table 2) fits a pattern gleaned from earlier research. Highest levels of white ash regeneration have been reported in the Midwest (Den Uyl 1961, Sander and Clark 1971, Parker and Leopold 1983, Boerner and Cho 1987, Martin and Hix 1988, Hix and Lorimer 1991, Roberts 1992). Relative to the Midwest, white ash regeneration declines to the west (Pallardy and others 1988, Shotola and others 1992), northeast (Hannah 1991, Smallidge and others 1991, Fain and others 1994, Volk and Fahey 1994), and southeast (Christensen 1977, Della-Bianca 1983, Clebsch and Busing 1989, Clinton and Boring 1994). Without a series of disturbance events that dramatically increases white ash regeneration density, white ash will gradually disappear from the forests in this study as mature trees die.

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